Why do Bulwer's Petrels *Bulweria bulwerii* change nest?

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Owning a nest is a prerequisite for breeding in Procellariiform seabirds, which can leave their single egg and/or chick unattended for long periods and show high nest fidelity. However, the determinants of nest fidelity vary among species. Amongst them, Bulwer's Petrel *Bulweria bulwerii* lays the biggest egg relative to body size within the Family Procellariidae. Therefore, individuals should choose their nests carefully and change essentially if they can improve their reproductive performances. This study conducted on Vila islet, Azores, aimed to determine why Bulwer's Petrels actually change nest. Nest fidelity exceeded 85%. Nest changes were most likely to occur after a breeding failure or a non-breeding year, but they did not allow improving breeding success and they often resulted in missed breeding years. On average, the new nests were not of higher quality than the old ones, except for the individuals whose first breeding attempt in the new nest was successful. In addition, the quality of the new nest was unrelated to the number of skipped years and to the distance moved. Almost half of changes occurred towards neighbouring nests. They were associated with a lower probability to skip years. Therefore Bulwer's Petrels might prioritize proximity over nest quality to reduce the costs of nest changes.

Key words: seabirds; nest fidelity; Bulwer's Petrel; *Bulweria bulwerii*; Azores

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INTRODUCTION

Obtaining a suitable territory/nest is a prerequisite to breeding in most bird species (Newton 1992). The choice of the breeding territory and/or the nest place and whether individuals should retain their breeding site the next breeding season or change are ultimately determined by breeding success, considering both previous and expected future reproductive performances (Greenwood & Harvey 1982; Switzer 1993).

Petrels (Order Procellariiformes) are a group of seabirds characterized by a very low fecundity (a single egg per breeding attempt without replacement in case of failure), deferred sexual maturity, high life expectancy (Warham 1990), and high year-to-year mate and nest fidelity

(review in Bried et al. 2003). Adults can perform long foraging trips during incubation and chick-rearing, leaving the chick (and sometimes the egg in the case of burrow-nesting species) unattended for several days (Warham 1990). Therefore, choosing a nest allowing the egg and the chick to remain alone without damage is crucial for these species, and nest changes are expected after poor reproductive performances. In addition, since Procellariiformes have part-time pair bonds (Morse & Kress 1984; Bried & Jouventin 2003), with partners migrating independently from each other and often spending the non-breeding period in distinct areas (Phillips et al. 2005; Catry et al. 2013; Weimerskirch et al. 2015), changing nest may imply changing mate. Therefore, individuals have to find a new nest, but also a new partner in

many cases, which may make nest changes extremely costly in terms of missed breeding years and/or increased mortality risk (see Bried & Jouventin 2002 for a review of the costs of nest and mate change). Nonetheless, the correlates of nest fidelity/change (i.e., reproductive performance, sex) differ among Procellariiform species (see e.g., Brooke 1978; Ollason & Dunnet 1988; Bried & Jouventin 1999; Jouventin & Bried 2001).

Bulwer's Petrel *Bulweria bulwerii* is a pantropical/subtropical cavity-nesting species (Megyesi & O'Daniel 2020) which lays the biggest egg relative to body size within the Family Procellariidae (Warham 1990). Given the energetic and metabolic costs of egg formation (Warham 1990), one can expect nest choice to be extremely important for this species, so that individuals would change nest only under particular, well-defined circumstances (see Switzer 1993). Nest fidelity in this species was studied by Mougin (1990, 1996, 1997) in the population from Selvagem Grande (north-eastern subtropical Atlantic). When determining the consequences of nest change, however, Mougin compared the reproductive performance at the new nest with respect to previous breeding experience but he did not examine the consequences in terms of missed breeding years, improvement of reproductive performance or quality of the new nest.

The population from Vila islet, Azores archipelago, seems especially suitable for examining the correlates and the consequences of nest change in this species because (1) it represents the bulk (about 70-80%) of the Bulwer's Petrel population from the Azores (T. Pipa & V.C. Neves pers.comm.), (2) accessible nests, which can therefore be monitored, represent a very high proportion of the total estimated number of nests, (3) and the breeding habitat there is stable (Bried et al. 2021). Under these conditions, high nest fidelity is expected and individuals should change nest only if the scope for an improvement of their reproductive performances is high (Switzer 1993).

Therefore, the aims of this study were to identify the correlates and the consequences of nest change in the Bulwer's Petrels from Vila

islet, and also to determine whether individuals moved to higher-quality nests. To do this, I used data from a 11-year demographic survey.

STUDY AREA AND METHODS

Field work was conducted on Vila islet (36º55'N, 25º10'W; 0.08 km^2), off Santa Maria island, Azores archipelago, north-eastern subtropical Atlantic. The islet is situated approximately 1200 km NW of Selvagem Grande and holds *ca* 50 breeding pairs of Bulwer's Petrels (Monteiro et al. 1999; this study). The breeding cycle of Bulwer's Petrel lasts *ca* 106 days from laying until chick departure to sea. Both parents incubate their single egg and feed the chick (Megyesi & O'Daniel 2020; J. Bried & V.C. Neves unpubl. data).

Birds were monitored each year from 2002 to 2012 included, using capture-mark-recapture. The islet was prospected extensively each year from 2003 onwards. Adults were captured by hand in their nests during incubation and ringed for identification (or identified from their ring number), in the course of 12-14-day (from late June to early July) field sessions enabling the capture of both pair members in most cases. Chicks were ringed before fledging. Each monitored nest was marked using an individual number. Given the small size of the study population, all accessible nests (that is, 85-90% of the total estimated number of nests on the islet) were included in the monitoring. One hundred and sixty-six individuals (75 males and 91 females) could be sexed (see Bried et al. 2021 for more details).

Statistical analyses
Because the probabilities of changing nest, fledging a chick, and missing at least one breeding year versus no year upon a nest change can be considered as binary (yes/no) variables, I performed logistic regressions. Since (1) several years of data concerning reproduction were available for many individuals, and (2) some individuals had changed nest several times, logistic regressions for repeated measures were performed (GENMOD procedure, binomial

distribution, logit link; SAS Institute 2020) to determine whether (1) previous breeding experience (i.e., the number of previous breeding attempts) and previous reproductive performance were associated with nest change, (2) the outcome of the first breeding attempt in the new nest was associated with sex and the fact of skipping or not breeding years, and (3) whether sex and breeding experience could be associated with the probability to miss (vs not to miss) breeding years before breeding in the new nest. I used the 'repeated' statement of GENMOD, which allows an unequal number of measures, and results were obtained from the models using generalized estimating equations (GEE). When using GEEs, the mean response depends on the independent variables and the parameter estimates describe the effects of the explanatory variables on the population (unlike Generalized Linear Mixed Models, which produce conditional estimates).

When determining the costs of nest change in terms of missed breeding years, it must be kept in mind that some individuals could skip several years. Therefore, and to avoid a bias in the distribution of missed breeding years due to individuals resuming breeding quickly after changing nest, the individuals that changed nest after 2006 were not considered. To determine the proportion of adult life expectancy represented by missed breeding years, I calculated life expectancy using Seber's (1973) formula, that is: adult life expectancy = $0.5 + [1/(1 - S)]$, S being the annual adult survival rate. The latter parameter was estimated at 0.8118 during this study (Abadi et al. 2014). Note also that two nest changes were excluded when analysing the consequences of nest changes (costs, reproductive performance) and the quality of the new nest, because it remains unknown whether the first one was associated with a breeding attempt in the new nest and whether the second one was performed by a single individual or a pair. All tests were two-tailed unless otherwise stated, and probability levels < 0.05 were considered significant.

Measures of nest fidelity and nest quality
Only adults (that is, birds known to have made at least one breeding attempt in the past) were used when calculating nest fidelity rates and determining the factors and the costs of nest change. Nest fidelity was defined as 1 minus the probability of nest change. The latter parameter was the number of observed changes divided by the theoretical number of changes if each adult changed nest every year it returned to the colony, independent of its breeding status (i.e., non-breeder, failed breeder, successful breeder) the previous year (Bried & Jouventin 2002).

To assess nest quality, only the nests monitored for at least five years were considered, following e.g., Jouventin & Bried (2001), and I used two parameters: nest occupancy rate (i.e., the proportion of years a nest was occupied by a breeding pair), and nest productivity (defined as number of fledglings produced per year, following e.g., Bourgeois et al. 2014). These parameters were considered separately when conducting analyses.

RESULTS

Overall, the rate of nest fidelity was 85.7% (n = 623 individual × years; actually 98 nest changes were observed during this study, see below; but nine of them were excluded here because I did not know exactly how many years the individuals that made them had returned to their former nest before changing), and did not differ significantly between sexes (G-test, $G_1 = 0.01$, P = 0.94, n = 271 male × years and 217 female × years). When examining the potential determinants or correlates of nest change, sex and breeding experience did not influence nest change, contrary to previous reproductive performance, failed breeders and non-breeders (i.e., sabbatical individuals) being most likely to change nest the next year (Table 1; similar results were obtained after considering only the individuals that changed nest without their former partner). 75.8% of the 91 nest changes for which the reproductive performance during the last year in the old nest was known occurred after a breeding failure or a non-breeding year. Note also that as previously mentioned by Bried et al. (2021), the breeding habitat was stable during this study. Indeed, only three nests became unsuitable for breeding (one nest was destroyed after being excavated by Cory's Shearwaters *Calonectris borealis*,

Table 1. Correlates of nest change in the Bulwer's Petrels from Vila islet (GENMOD, analysis of GEE parameter estimates, n = 103).

Parameter	Estimate	95% confidence interval	Z	P
Intercept	-2.385	-3.705 - -1.065	-3.54	0.0004
Sex: female	-0.739	-1.916 - 0.438	-1.23	0.219
Previous reproductive performance				
Non-breeder	1.423	0.062 - 2.784	2.05	0.040
Failed breeder	1.739	0.361 - 3.117	2.47	0.013
Breeding experience	-0.069	-0.381 - 0.244	-0.43	0.667

The first levels of the variables "Sex" (here, male) and "Previous reproductive performance" (here, successful breeder) were used as baselines. Breeding experience here was expressed as the number of previous breeding attempts, but similar results were obtained after considering first-time breeders versus more experienced breeders.

and the two other nests were taken over, the one by Common Starlings *Sturnus vulgaris granti* and the other by feral Rock Pigeons *Columba livia*).

Distance between the old and the new nest
Of the 98 observed nest changes, 34.7% occurred towards the nearest neighbouring nest and 43.9% to one of the two nearest neighbouring nests. 29.6% were associated with long-distance movements, ranging from 20 to 100 m. When considering only the 62 nest changes followed by a breeding attempt in the new nest, those towards the nearest neighbouring nest represented 38.7% of cases, those towards one of the two nearest neighbouring nests represented 50% of cases, and 33.9% of changes occurred to nests situated between 20 and 100 m from the old nests (Table 2).

As already reported by Bried et al. (2021), 13 pairs changed nest together, but only 11 bred in their new nest. Amongst the latter, seven moved to the nearest neighbouring nest, which was situated between 0.3 and *ca* 10 m from the old nest. Interestingly, one pair returned to their old nest after spending only one year in their new one. This year, the old nest was occupied by a non-breeding pair. One pair moved to the second nearest neighbouring nest. The remaining three pairs moved to more distant nests (range: ~5-30 m from the previous nest, see Table 2).

Table 2. Distances moved during nest changes. In parentheses: nest changes associated with a breeding attempt in the new nest. Concerning the calculations made when referring to this Table: one pair changing nest corresponds to two individuals changing nest, therefore two changes were counted.

	Pairs	Solitary individuals
Changes to the nearest neighbouring nest	10 (8)	14 (8)
Changes to the second nearest neighbouring nest	1 (1)	10 (5)
Changes to a more distant nest	3 (3)	46 (25)

Sixty-seven nest changes were performed by individuals that had lost their former partner (i.e., after its death or a divorce). Fourteen of them occurred towards the nearest neighbouring nest, and five of them occurred to the second nearest neighbouring nest. Interestingly, a male that changed nest after a divorce returned to his old nest, where it was observed with another individual two years later during the chick-rearing period, after the pair that had taken the nest over had failed to hatch their egg. The next year, the new pair performed their first breeding attempt. Another male moved, lost its partner (which

presumably died) and returned to its old nest after spending a sabbatical year.

When considering the nest changes associated with a breeding attempt in the new nest, the individuals that retained their partner moved to one of the two nearest neighbouring nests significantly more often than those that changed singly (18 out of 24 cases vs 13 cases out of 38; G-test with Williams' adjustment, $G_{1W} = 9.878$, P = 0.002). Amongst the latter, males were not more likely to move to the nearest neighbouring nest or to one of the two nearest neighbouring nests than females (males: three cases and seven cases, respectively, n = 18; females: one and two cases, respectively, n = 14; G_{1W}, both P > 0.12).

Consequences of nest changes for reproduction
All changes associated with a breeding attempt in the new nest
During the first breeding attempt in the new nest, and regardless of whether nest change was associated with mate retention or the loss of the previous partner, the individuals that were first-time breeders before changing nest tended to have a higher breeding success (61.5%, n = 13 cases) than more experienced individuals (41.7%, n = 36 cases) but the difference was not significant (G-test with Williams' adjustment, $G_{1W} = 1.458$, P = 0.227). Overall, the probability to fledge a chick upon the first breeding attempt in the new nest was not related to sex, previous breeding experience, mate retention or loss, the fact of skipping or not skipping years before breeding in the new nest, and to whether the new nest and the old nest were neighbouring nests or distant nests (Table 3).

Nest changes made by pairs
Pairs skipped between zero and two (perhaps three in two cases) years before breeding in the new nest. In the five instances where they skipped at least one year, the new nest was the nearest neighbouring nest in two cases and a distant nest in three cases. In the seven instances where pairs missed no year before breeding in their new nest, the new nest was the nearest neighbouring nest in six cases and the second nearest neighbouring nest in the seventh case. The difference between the two categories of pairs was significant (changes towards the two nearest neighbouring nests vs towards more distant nests, Fisher's exact test, P = 0.045).

Nest changes made by pairs were not associated with better reproductive performances in the new nest (Wilcoxon matched pairs signed rank test, $T_- = 2.5$, n = 4, P > 0.1), and whether or not pairs had missed breeding years did not seem to influence the outcome of the first breeding attempt in the new nest either (Mann-Whitney U, $n_1 = 5$, $n_2 = 7$, P > 0.2).

Nest changes made by solitary individuals (i.e., divorcees and widowers)
The individuals that moved singly spent on average 2.43 years ± 0.46 SE (n = 18) before resuming breeding. This value, which represented 41.7% of adult life expectancy, did not differ significantly between sexes (Mann-Whitney U = 32.5, n = 8 males and 9 females, P > 0.2; the nest changes occurring after 2006 were excluded from the analysis, see Methods). The divorcees and widowers that changed nest also tended to miss more years than the individuals that changed nest with their partner, the difference being almost significant (Mann-Whitney U = 24, $n_1 = 6$, $n_2 = 18$, P = 0.05; the nest changes occurring after 2006 were excluded). Still after excluding the nest changes occurring after 2006, solitary and paired individuals missed significantly fewer years when they moved to one of the two nearest neighbouring nests (0.75 year ± 0.53 SE, n = 8) than when they moved towards a more distant nest (2.56 years ± 0.47 SE, n = 16; Mann-Whitney U = 25, P < 0.025).

The solitary individuals that had missed no year before breeding in their new nest had moved to the nearest neighbouring nest (four cases) or the second nearest neighbouring nest (two cases, vs two shifts towards more distant nests) more often than those that had skipped at least one year upon nest change (five cases and three cases, respectively, out of 30). The difference was significant whether changes towards the nearest neighbouring nests and changes towards the second nearest neighbouring nests were pooled together or considered separately (G-test, $G_{1W} = 5.803$, P = 0.016, and $G_2 = 6.25$, P = 0.044, respectively).

Table 3. Factors influencing breeding success upon the first breeding attempt in the new nest in Bulwer's Petrels (GENMOD, analysis of GEE parameter estimates, n = 30).

Parameter	Estimate	95% confidence interval	Z	P
Intercept	0.201	-1.536 - 1.938	0.23	0.820
Sex: female	0.509	-1.902 - 0.884	0.72	0.474
Missed breeding years: no	-0.602	-2.227 - 1.022	-0.73	0.467
First-time breeder	0.225	-1.687 - 2.138	0.23	0.817
Distance between old and new nest: distant nests	0.520	-1.159 - 2.199	0.61	0.544
Moved with its partner	-0.235	-1.722 - 1.252	-0.31	0.757

The first levels of the variables "Sex" (here, male), "missed breeding years" (here, at least one missed year), "previous breeding experience" (here, yes),"distance between the old and the new nest" (here, nearest neighbouring nest or second nearest neighbouring nest), and "moved with its partner or moved singly" (here, moved singly) were used as baselines.

When nest changes occurred towards nests more distant from the old nest than were the two nearest neighbouring nests, the distance moved ranged to less than five metres to almost 100 metres. When controlling for potentially confounding factors that might affect the number of missed breeding years upon nest change, the probability to miss at least one breeding year before breeding in the new nest did not depend on sex or on whether individuals were first-time breeders or more experienced before changing (Table 4; similar results were obtained after controlling for whether the new nest was one of the two nearest neighbouring nests from the old nest or a more distant nest).

Like for pairs, breeding performance upon the first breeding attempt in the new nest was not significantly higher to that (1) during the last year in the old nest, regardless of whether or not sex was taken into account (all individuals: 0.51 chick $\pm$ 0.09 SE, n = 34, vs 0.31 $\pm$ 0.06 SE, n = 54, in the old nest; Wilcoxon matched pairs signed rank test, all P > 0.05) and (2) during the last breeding attempt in the old nest (0.35 chick $\pm$ 0.07 SE, n = 53; Wilcoxon matched pairs signed rank test, all P $\geq$ 0.2, still regardless of whether or not sex was

taken into account). Also, it did not depend on whether or not the new partner was experienced (Fisher's exact test, n = 29, P = 0.71). The second breeding attempt in the new nest was not more successful than the first one (in 15 cases out of 18, the outcome was the same as during the first breeding attempt).

Quality of the new nest
Overall, the quality of the new nests chosen by pairs did not differ significantly from that of the old nests (Wilcoxon matched pairs signed rank test on occupancy and productivity, both n = 9 and P > 0.2). The individuals that changed nest without their former partner settled on nests whose productivity was also similar to that of the old nest (Wilcoxon matched pairs signed rank test, n = 26, P > 0.2), but whose occupancy rate was significantly higher than in the old nest (Wilcoxon matched pairs signed rank test, T_+ = 88, n = 25, P < 0.05). However, the significance of the difference was actually due to the individuals whose first breeding attempt in the new nest was successful. Indeed, only these individuals obtained significantly higher-quality nests compared to their old nests (occupancy:

Table 4. Factors determining whether or not the Bulwer's Petrels that changed nest without their former partner missed breeding years upon nest change (GENMOD, analysis of GEE parameter estimates, n = 22).

Parameter	Estimate	95% confidence interval	Z	P
Intercept	0.631	-0.647 - 1.909	0.97	0.333
Sex: female	0.646	-1439 - 2.731	0.61	0.544
Previous breeding experience: first-time breeder	0.398	-2.071 - 2.867	0.32	0.752

The first levels of the variables "Sex" (here, male) and "Previous breeding experience" (here, experienced individual) were used as baselines.

0.580 ± 0.058 SE, n = 16, vs 0.314 ± 0.051 SE, n = 16; Wilcoxon matched pairs signed rank test, $T_+ = 7$, n = 12, P = 0.01; productivity: 0.367 ± 0.049 SE, n = 15, vs 0.128 ± 0.033 SE, n = 16; Wilcoxon matched pairs signed rank test, $T_+ = 0$, n = 13, P < 0.001).

No correlation was found between nest occupancy or productivity and the number of missed years when changing nest (Spearman rank correlation, pairs: both n = 9 and P > 0.09; individuals that moved singly: occupancy: n = 29, productivity: n = 28, both P > 0.75), and the quality of the new nest was not related to the fact of missing breeding years or not either (pairs: Mann-Whitney U, $n_1 = 4$, $n_2 = 5$, both P $\geq$ 0.2; individuals that moved singly: Mann-Whitney U, $n_1 = 6$, $n_2 = 25$, both P > 0.25).

When an individual that changed nest after losing its partner resumed breeding, it was not more or less likely to settle on a higher quality nest when the old nest and the new one were neighbouring nests (nearest neighbouring or second nearest neighbouring nest) than when they were more distant from each other (occupancy rate and productivity after pooling Categories "higher" and "equal" together, see Table 5; G-test with Williams' adjustment, G_{1W}, both P > 0.17). Unfortunately, small sample size precluded reliable results when examining the correlates of breeding success in the new nest after adding nest quality amongst the explanatory variables listed in Table 3.

DISCUSSION

Correlates of nest change

High nest fidelity on Vila islet may be explained by the high overall persistence of the nests from one year to the next (Bried et al. 2021; see also Mougin 1990, 1996). On Selvagem Grande, Mougin (1996) also observed a high nest fidelity in an area where the nesting habitat was stable (87.9%), but not in a more unstable area (67.7%). Similarly, Bourgeois et al. (2014) explained (at least, partly) the high nest fidelity observed in Yelkouan Shearwaters *Puffinus yelkouan* (94.7%) by the stability of the nesting habitat, whereas Mariné & Cadiou (2019) explained the high nest fidelity of European Storm-petrels *Hydrobates pelagicus* (94%) by the quality of the nests as shelters.

As expected by theory when the breeding habitat is stable (Switzer 1993), nest changes in the Bulwer's Petrels from Vila islet were generally associated with poor reproductive performance the previous year, as also found in other petrel species (e.g., Mougin et al. 1987; Bourgeois et al. 2014; Mariné & Cadiou 2019; but see Jouventin & Bried 2001). Nonetheless, they did not lead to a significant improvement of breeding success, similarly to what occurs in Yelkouan Shearwaters (Bourgeois et al. 2014) and European Storm-petrels (Mariné & Cadiou 2019), but contrary to Snow Petrels *Pagodroma nivea* (Jouventin & Bried 2001).

Table 5. Quality of the new nest compared with that of the old nest for the individuals that moved singly and bred in their new nest.

	Higher	Equal	Lower
Occupancy			
Nearest or second nearest neighbouring nest	5	4	1
More distant nest	14	1	7
Productivity			
Nearest or second nearest neighbouring nest	6	0	3
More distant nest	12	3	2

In addition, and contrary to theory (e.g., Curio 1983) and to what Mougin (1997) observed on Selvagem Grande, the individuals that were first-time breeders before changing nest did not experience more breeding failures than more experienced individuals upon their first breeding attempt in the new nest. I have no explanation concerning the latter phenomenon. Conversely, the absence of relationship between nest fidelity and breeding experience (a potential confounding factor given that breeding success often increases with experience in birds, Lack 1968; Rowley 1983) is not so surprising given that reproductive performances do not improve with pair breeding experience in the Bulwer's Petrels from Vila islet (Bried et al. 2021).

Like their conspecifics from Selvagem Grande (Mougin 1996) and also other petrel species (e.g., Cory's Shearwater, Mougin 2002; Snow Petrel, Jouventin & Bried 2001; Yelkouan Shearwater, Bourgeois et al. 2014; European Storm-petrel, Mariné & Cadiou 2019), male Bulwer's Petrels were as likely as females to change nest on Vila islet. When nest changes were followed by a breeding attempt with a new partner, they were also as likely as females to move towards neighbouring nests or towards more distant nests, like the Cory's Shearwaters from the same location (Bried et al. 2010). In contrast, Mougin et al. (1987) found that male Cory's Shearwaters moved to neighbouring nests more often than females during the nest changes associated with re-mating on Selvagem Grande, and Kim et al. (2007) found that in the Blue-footed Booby *Sula nebouxii*, a non-Procellariiform seabird, males also moved shorter distances than females during the nest changes following divorces.

Nonetheless, nest changes in Bulwer's Petrel were not always associated with partner loss. Indeed, more than one third of the nest changes associated with a breeding attempt in the new nest were performed by individuals that retained their previous partner, on Vila islet (Bried et al. 2021; this study) as well as on Selvagem Grande (Mougin 1996). The fact that nest change is not always associated with pair bond disruption has also been observed in other seabird species, including non-Procellariiform species (Bried et al. 2003 and references therein; Bried et al. 2010; Bourgeois et al. 2014; Mariné & Cadiou 2019), strongly suggesting that mate fidelity does not solely arise from nest fidelity, but is an active process, even in species with part-time pair bonds (see Bried et al. 2003).

Distance moved and costs of nest change
Less than 40% of nest changes occurred towards the nearest neighbouring nest. This pattern is similar to those observed in Cory's Shearwaters (on Vila islet, 42.5% of nest changes associated with a breeding attempt with a new partner occurred to the nearest neighbouring nest and 14.9% to the second nearest neighbouring nest, Bried et al. 2010; on Selvagem Grande, 50% of nest changes associated with the loss of the previous partner occurred towards the nearest neighbouring nest, Mougin et al. 1987), and in Yelkouan Shearwaters (the individuals that

changed nest moved to the nearest neighbouring nest in 28.6% of cases, and could move up to 60 m far from their previous nest, Bourgeois et al. 2014). The non-negligible proportion of changes to very distant nests on Vila islet (that is, situated more than 20 m far from the old nest) may be explained by the low nest density at this locality (Bried at al. 2021).

Nest changes were extremely costly in terms of missed breeding years (especially for the individuals that changed nest after losing their partner), even when considering the Order Procellariiformes where skipping breeding years after a divorce or a nest change is not uncommon (Bried 2000; Jouventin & Bried 2001; Bried et al. 2010; Bourgeois et al. 2014).

Like in the Cory's Shearwaters from Selvagem Grande (Mougin et al. 1999), long-distance movements were more frequently performed by individuals that moved after losing their partner than by pairs, which moved to neighbouring nests more often than did widowers and divorcees and for which the distance between the old and the new nest did not exceed 30 metres. The number of missed breeding years upon nest change was lower when the old nest and the new nest were neighbouring nests than when they were distant nests, and the pairs and the solitary individuals that missed no breeding years settled more often in a neighbouring nest than in a more distant nest when compared to those that missed at least one breeding year. Therefore, changing towards neighbouring nests might help Bulwer's Petrels to reduce the costs of nest change, possibly because the availability of neighbouring nests at a given moment is easier to assess than in more distant nests. A similar hypothesis was invoked by Mougin et al. (1988a, b; 2001) to explain why divorced and widowed Cory's Shearwaters tended to re-mate preferentially with neighbours, whose quality would be easier to assess than for individuals occupying more distant nests. However, divorced and widowed Bulwer's Petrels do not preferentially form new pair bonds with neighbours on Vila islet (Bried et al. 2021).

The absence of a relationship between the quality of the new nest and the number of missed years before breeding in the new nest suggests that Bulwer's Petrels do not trade off the costs of nest change against nest quality and do not "wait" (see Ens et al. 1995) before eventually obtaining high quality nests, even though the individuals that obtain such nests have greater chances to breed successfully. However, the definition of nest quality in this study may be incomplete given that the quality of a nest may be confounded, at least partly, by that of its occupants. On the other hand, the hypothesis that high quality nests are those where breeding attempts are most likely to succeed regardless of pair quality cannot be dismissed either. Further research is needed to determine the characteristics of such nests (e.g., rock and/or vegetation cover, chamber dimensions and substrate, entrance orientation; see Bourgeois et al. 2014; Fagundes et al. 2016).

Conclusion

Although the probability of changing nest in the Bulwer's Petrels from Vila islet increased after a failure to fledge a chick, reproductive performances were not significantly better in the new nest. Furthermore, nest changes were extremely costly in terms of missed breeding years, but changing towards neighbouring nests might enable individuals and the pairs that moved together to reduce these costs. The quality of the new nest was independent of the distance moved and of the number of missed years, and pairs (which are likely to have a competitive advantage compared to solitary individuals) moved to neighbouring nests more often than did divorcees and widowers, suggesting that Bulwer's Petrels prioritize proximity over quality when changing nest. Supporting this, the new and the old nest on Selvagem Grande, where the overall breeding density of Bulwer's Petrels is almost three times higher than on Vila islet (Bried et al. 2021), are generally situated a few metres apart (Mougin 1996).

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